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Yet while this is true, the platforms in Fiji are post-Pleistocene in their development. The writer was unable to discover any evidence of Pleistocene wave-cut platforms.

<sup>1</sup> Woolnough, W. G., *Sydney, Proc. Linn. Soc. N. S. Wales*, 32, 1907 (431-474).

<sup>2</sup> Guppy, H. B., *Observations of a Naturalist in the Pacific*, vol. 1, Macmillan, 1903.

<sup>3</sup> Gerland, G., *Beitr. Geophys.*, Leipzig, 2, 1895, (56).

<sup>4</sup> Daly, R. A., *Boston, Proc. Am. Acad. Arts Sci.*, 51, 1915, (157-251), p. 232.

<sup>5</sup> Vaughan, T. W., *Washington, J. Acad. Sci.*, 6, 1916, (53-66).

## DOMINANCE OF LINKED FACTORS AS A MEANS OF ACCOUNTING FOR HETEROSIS

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Communicated by W. M. Wheeler, February 26, 1917

The increase of growth derived from crossing in both animals and plants, which has been called heterosis, and the converse fact of decreased vigor resulting from inbreeding have been known for a long time but have never been satisfactorily accounted for.

The investigations of East,<sup>2</sup> G. H. Shull<sup>3</sup> and Hayes<sup>4</sup> show that inbreeding does not result in a continuous degeneration but that the effects of inbreeding gradually become less as complete homozygosis is approached and for all practical purposes finally become constant. Unlike strains are isolated which differ in the amount of growth they produce. In many species these homozygous strains are always less vigorous than either parent. The decrease in vigor due to inbreeding has been shown to be correlated approximately with the decrease in the number of heterozygous factors present but without showing why there should be such a relation. It was simply stated that "greater developmental energy is evolved when the mate to an allelomorphic pair is lacking than when both are present in the zygote."<sup>4</sup>

The conception of dominance as proposed by Keeble and Pellew<sup>5</sup> as a means of accounting for these facts has had two serious objections. If heterosis were due to dominance of characters it was thought possible to recombine in generations subsequent to the  $F_2$  all of the dominant characters in some individuals and all the recessive characters in others in a homozygous condition. Such homozygous individuals could not be changed by inbreeding. Moreover, if dominance were concerned it was considered that the  $F_2$  would have an asymmetrical distribution.

Both of the above objections to dominance have failed to take into consideration the facts of linkage. If the factors which govern an organism's development are distributed in all the chromosomes and passed

from one generation to another in groups it would be practically impossible to recombine all the dominant characters in one individual and all the recessive in another. Hence the failure to obtain both the complete dominants and complete recessives which would breed true is accounted for. This view of the situation also explains why symmetrical distributions are obtained in  $F_2$ . The development of each individual is assumed to be correlated with the number of different factors present. The individual with the greatest number of heterozygous chromosomes would have the greatest number of different factors present if the factors were distributed among all the chromosomes. The theoretical distribution of the  $F_2$  individuals according to the number of heterozygous chromosomes contained is in the ratio of the expanded binomial  $(a+a)^n$ . The expanded binomial is often used as an illustration of a normal frequency distribution.

To account for the increase in growth in  $F_1$  it is necessary to have the favorable characters for the most part dominant over the unfavorable ones. This seems probable from the numerous cases of abnormalities which are recessive to the normal condition. It is not necessary that there should be perfect dominance. It is necessary, however, to accept the conclusion that *many factors in the 1n condition have more than one half the effect that they have in the 2n condition*.

Inbred strains of maize have been obtained by inbreeding which either lack chlorophyll entirely or are partially deficient in chlorophyll. Some strains are partially sterile. Some have fasciated ears. Some are susceptible to a bacterial wilt disease. Some have contorted stems and still others have brace roots so poorly developed that they can not stand upright when the plants become heavy. Similar instances can be cited in many naturally cross pollinated species. Some of the strains may have more than one of these unfavorable characters. No one strain so far known has them all.

Crossing these strains together gives perfectly normal  $F_1$  plants. They are able to grow better than their parents because the characters necessary for maximum development that one strain lacks are supplied by the other and conversely. This increased growth is heterosis.

Dominance of characters gives a reason why heterozygosis should cause the  $F_1$  generation to grow more than the parents and not less. According to previous views it would have been just as reasonable to suppose that hybridization had a depressing or an indifferent rather than a stimulating effect. It also makes it easier to understand why heterozygosis should operate throughout the life of the individual even through innumerable generations of vegetative propagation.

This conception of dominance of linked factors to account for the facts as so far known does not preclude the possibility of a physiological effect resulting from hybridization apart from hereditary factors if such an effect can be demonstrated. It simply coördinates the existing knowledge of heredity to give a comprehensible view of the way in which heterosis may be brought about.

<sup>1</sup> Contribution from the Connecticut Agricultural Experiment Station and the Bussey Institution of Harvard University.

<sup>2</sup> East, E. M., *Connecticut Agric. Exp. Sta. Rep.*, 1907, 1908, (419-428); *Amer. Nat., Lancaster, Pa.*, 43, 1909, (173-181).

<sup>3</sup> Shull, G. H., *Amer. Breeders Assoc. Rep.* 4, 1908, (296-301); *Amer. Nat., Lancaster, Pa.*, 45, 1911, (234-252).

<sup>4</sup> East, E. M., and Hayes, H. K., *U. S. Dept. Agric., Bur. Plant Ind. Bull.* No. 243, 1912.

<sup>5</sup> Keeble, F., and Pellew, C., *J. Genetics, Cambridge*, 1, 1910, (47-56).

## CHEMICALLY INDUCED CROWNGALLS

By Erwin F. Smith

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In 1911 in Bulletin 213 on "Crown Gall of Plants: its Cause and Remedy" (Bureau of Plant Industry, U. S. Dept. of Agric.) I expressed the conviction that while the disease was clearly due to *Bacterium tumefaciens* we would eventually be able to go a step farther (i.e., p. 175) and determine just what by-products of the organism were the direct cause of the over-growth. With this end in view, on several occasions I prepared flask cultures of the organism for use of the chemist of the Department and with substances said by him to be present in the culture flasks and absent from the controls I have recently made experiments which tend to confirm my earlier supposition and expectation.

It is not maintained for a moment that these are the only substances that are able to cause overgrowths in plants but only that they are the most interesting ones in that they are the products of a cancer parasite, or, if one prefers so to express it, of a schizomycete which is the cause of a plant tumor possessing many features in common with animal cancers.

The substances produced by *Bacterium tumefaciens* in very simple culture media, i.e., in flasks of distilled water containing 1% dextrose and 1% peptone with a little calcium carbonate added to neutralize any acids formed and thus to favor long continued growth since the crown gall organism is very sensitive to its own acid products, are—alde-